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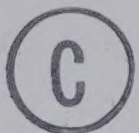
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MICROENVIRONMENT AND WATER RELATIONS
OF TWO ALPINE SPECIES,
OLYMPIC NATIONAL PARK

by



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A THESIS

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ABSTRACT

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A summer-dry climate and rain shadow created by the central Olympic Mountains result in very low precipitation in the eastern Olympic Mountains, Washington, U.S.A. This study, in the summer of 1969, attempted to characterize the microenvironment and water balance

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Microenvironment and Water Relations of Two Alpine Species, Olympic National Park", submitted by Sheila Mae Peterson in partial fulfillment of the requirement for the degree of Master of Science.

ABSTRACT

A summer-dry climate and rain shadow created by the central Olympic Mountains result in very low precipitation in the eastern Olympic Mountains, Washington, U.S.A. This study, in the summer of 1969, attempted to characterize the microenvironment and water balance of two alpine species on Elk Mountain, in the eastern Olympic Mountains. Microenvironmental parameters (wind, and solar radiation, temperature, vapor pressure deficit and soil moisture) were recorded. Especially notable was the low summer precipitation (less than 2.5 cm during the ten week study). In general, winds were light (2 to 3 m/sec), temperatures low (9°C), and solar radiation (520 ly/day) and vapor pressure deficit (2.3 mmHg) moderate. Profiles of air and soil temperature, vapor pressure deficit and wind, as well as leaf temperatures, were taken in relation to the two species studied, *Lupinus lepidus* var. *lobbii* and *Synthyris pinnatifida* var. *lanuginosa*. These measurements indicated restriction of transpiration. Leaf water potentials of *Lupinus* and *Synthyris* were measured with a pressure bomb for seasonal and diurnal trends. *Lupinus* maintained a fairly constant Ψ_{leaf} at -16 bars. *Synthyris* had lower Ψ_{leaf} values (-25 bars) which increased in September, following a rainy period. The Ψ_{leaf} of *Synthyris* appears to be correlated to the moisture in the upper level (10 to 15 cm) of the soil. Morphological studies showed some xeromorphic characters such as hairy leaves, high root:shoot ratios and folded leaflets. A comparison of the two species showed *Lupinus* to be in better balance with available moisture, based on Ψ_{leaf} values and lower leaf temperature; while *Synthyris* was apparently better adapted for period of water stress on the dry ridge top, judged by xeromorphic features and the ability to grow with low leaf water potentials.

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INTRODUCTION

The alpine environments in North America have extremely variable moisture regimes. In the east, the New England mountains have a humid climate, as is the case in many alpine areas throughout the world (Major and Bamberg 1967, Tranquillini 1963). In the western United States there is increasing summer drought; the Rocky Mountains have a slight summer drought, and the Sierra Nevada a considerable one (Major and Bamberg 1967). The summer dry period occurs in the Olympic Mountains also, especially east of the Bailey Range and Mount Olympus (Fig. 1), due to rain shadow and regional climatic patterns (Fonda and Bliss 1969, Kuramoto 1968).

During the dry summer of 1967, many individuals of *Lupinus lepidus* var. *lobbii**, a common plant of Elk Mountain in the eastern Olympic Mountains, died, apparently from drought (Bliss personal communication) (Fig. 2). Since then it has become re-established. Other plants were not noticeably affected by the drought.

This study was carried out to characterize the micro-environment of the Elk Mountain ridge top and monitor certain parameters related to the water and heat (energy) budgets of *Lupinus lepidus* var. *lobbii* and *Synthyris pinnatifida* var. *lanuginosa*. This was done to determine the nature of drought resistance of the two plants and to attempt to explain the differential response of the two species to the 1967 drought.

*Nomenclature follows Hitchcock et al. (1961).

Figure 1
OLYMPIC PENINSULA

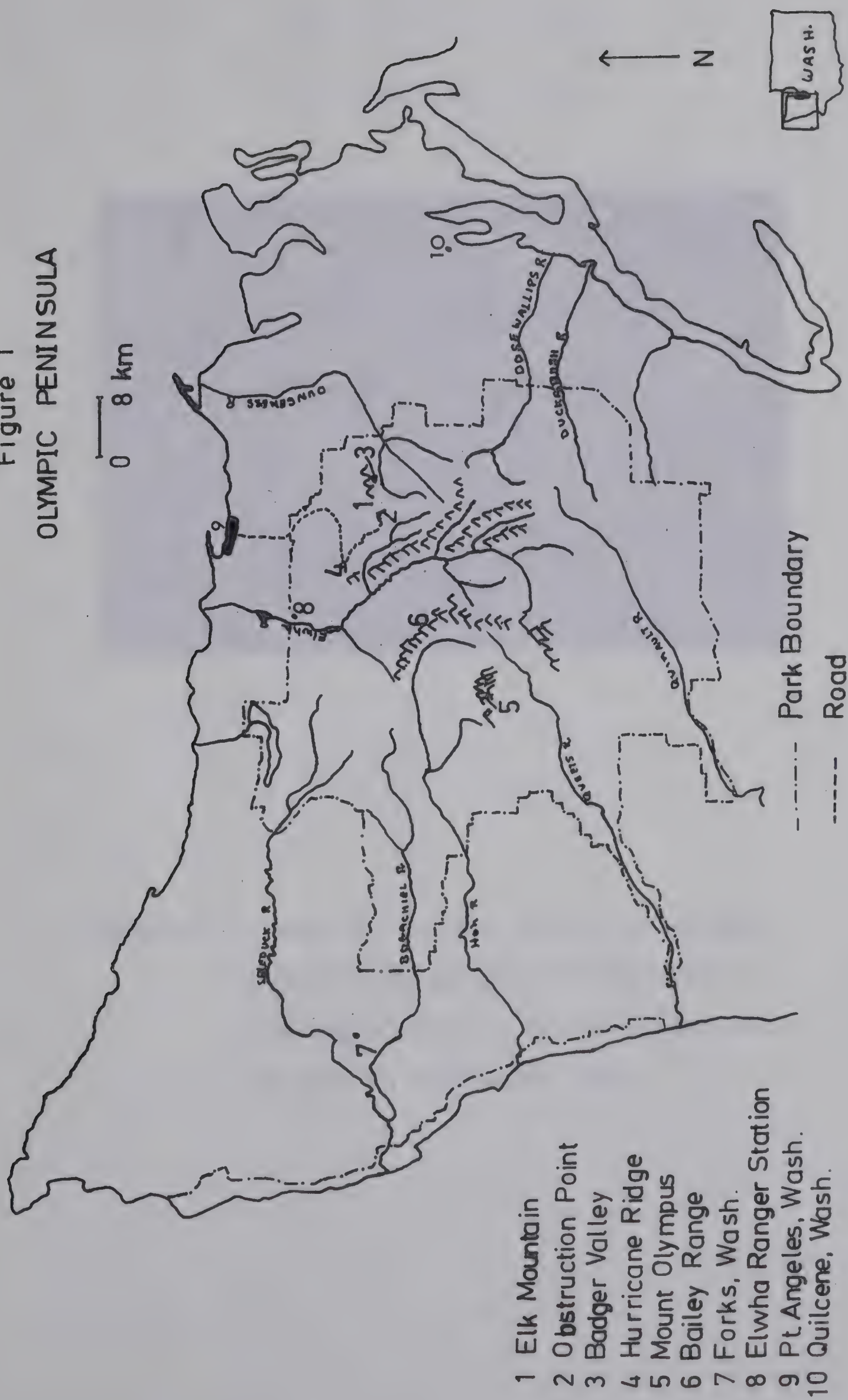




FIGURE 2: Clumps of *Lupinus* killed by drought in 1967 can be seen in the center and upper center. A live clump can be seen in the lower right.

DESCRIPTION OF STUDY AREA

Olympic National Park

Physiography

Olympic National Park is located on the Olympic Peninsula in western Washington. The main portion of the Park is in the central mountainous area of the Peninsula. The mountains are the result of several uplifts, foldings, and mild metamorphoses of marine sedimentary and volcanic deposits since the Cretaceous Period. Soleduck and Metchosen Formations, composed of shales and fine-grained sandstones, are the main rock components of the eastern mountains. In general, the mountains trend northwesterly to southeasterly, with the highest peaks in the central portion. Mt. Olympus, the highest peak, rises to 2417 m, and other peaks exceed 2000 m.

The mountains are drained into the nine rivers, the largest being the Elwha River which flows to the north. The valleys along the west-flowing rivers, Queets, Quinault and Hoh, are covered by the Olympic Rain Forest.

Vegetation

The vegetation of the Peninsula is largely coniferous forest (Bliss, et al 1969). Valley forests along the rivers of the western Olympic Mountains, the Olympic "Rain Forest", are a mixed forest of *Picea sitchensis*, *Tsuga heterophylla*, *Acer macrophyllum*, *Populus trichocarpa*, and *Alnus rubra*. The deciduous trees are mainly successional and are found on first river terraces and new river bars. The trees are mixed with conifers. On second and third terraces, *T. heterophylla* and *P. sitchensis* are dominant, hardwoods are absent. The transition

from mixed wood can occur in so small a rise as 6 m from first terrace to the second. *Thuja plicata* and *Pseudotsuga menziesii* are on steeper slopes of valley walls. *Abies amabilis*-*Tsuga heterophylla* forests dominate the western part at mid-elevations; to the east, *Tsuga heterophylla* and *Pseudotsuga menziesii* forests predominate. Subalpine forests at 1100 to 1650 m in the west ranges and between 1300 and 1800 m in the east ranges are composed of *Abies amabilis* and *Tsuga mertensiana* on the western slopes; while on drier, eastern slopes, *Abies lasiocarpa* dominates (Fonda and Bliss 1969).

Subalpine meadows occur at the upper limit of the subalpine forest. They are between scattered family grouping of *A. lasiocarpa* or *T. mertensiana*, either snow basins or open areas created by fire, have been described by Kuramoto (1968) who recognized eight community types. The cushion plant community found on relatively steep, windy, south-facing slopes in the Hurricane Ridge area is most similar to the alpine ridge community of the study area. Species peculiar to this meadow are *Arabis canescens*, *Collensia parviflora*, *Douglasia laevigata* and *Erysimum arenicala* var. *torulosum*. Common cushion plants include *Phlox diffusa*, *Arenaria capillaris*, *Douglasia laevigata* and *Pachistima myrsinites*. The other community types include Dry Grass-Forbs Meadow, Mesic Grassy Meadow, *Saussurea* Moist Meadow, *Valeriana* Moist Meadow, Tall Sedge Meadow, Heath Shrub Meadow, and Dwarf Shrub Meadow.

In alpine communities on slopes and exposed areas above tree line at ca. 1800 m, Bliss (1969) found plants in scattered clumps and strips. Species here include *Phlox diffusa*, *Arenaria obtusiloba*, *Draba lonchocarpa*, *Synthyris pinnatifida*, *Carex albonigra*, and *Potentilla diversifolia*. In less exposed areas which have a greater snow cover,

herb meadows occur. *Carex phaeocephala*, *Potentilla diversifolia*, *Phlox diffusa*, *Draba lonchocarpa*, and *Solidago spathulata* predominate in these areas. Alpine vegetation is mostly restricted to mountains in the northeast portion of the Park at elevations of 1800 to 2400 m (Bliss 1969). Although mountains to the west and south of this area are high enough to support alpine communities, vegetation is limited by sheer rocky slopes and snow and ice.

Climate

The climate of the Peninsula, due to the maritime influence, has mild temperatures year round. As reported by Kuramoto (1968) and Fonda and Bliss (1969), mean annual temperature range is narrow: Forks, Washington (Fig. 1), on the west coast, has a temperature range of 14.6°C (3.7° to 18.3°); Elwha Ranger Station to the east has a range of 16°C (1.2° to 17.5°); and east of the mountains, Quilcene has a mean temperatures range of 14.8°C (2.7° to 17.5°). Summer temperatures range from 18° to 24°C during the day to a low of 10°C at night at low elevations. In winter, the range is generally from 4° or 8° to -1°C.

Maximum precipitation occurs in winter; summers are relatively dry. In summer, high pressure systems are centred over the Hawaiian Islands. The resulting northwesterly winds move onshore as they move south, and carry dry, cool, and rather stable air over the Peninsula. In winter, low pressure systems are centered over the Aleutian Islands. The southwesterly winds from the low pressure cells are moist, warm, and relatively unstable. When this air comes onshore and is forced to rise over the land and mountains, heavy precipitation is produced.

The north-south trend of the mountains prevents even distribution of precipitation. The peaks of the Bailey Range and Mt. Olympus (Fig. 1) create a barrier to the moist westerly winds and winter cyclonic storms. As a result, the eastern mountains are drier than might be expected in a maritime region. The windward position of some slopes, which cause them to be blown free of snow in winter, further enhances the dryness by loss of potential melt water in spring.

Further discussion of physiography, climate, geology and vegetation can be found in Bliss (1969), Fonda and Bliss (1969), Kuramoto (1968), Danner (1955), and Tabor (1969).

Elk Mountain

General Description

Elk Mountain is located in the northeastern part of Olympic National Park, 1 km from Obstruction Point and 12 km from Hurricane Ridge (Fig. 1). The mountain trends east and west. The study area was selected on a south-facing, windward slope (20%) on the western end of the mountain at 1972 m elevation (Fig. 3). At this site the soil is poorly developed from weathered shale and fine-grained sandstone of the Soleduck Formation. The vegetation, described by Bliss (1969) consists of clumps of cushion plants which grade into vegetation stripes lower down the slope as the inclination increases. *Phlox diffusa*, *Lupinus lepidus*, with *Synthyris pinnatifida*, and *Antennaria racemosa* are dominant species. *Carex albonigra* and *Potentilla diversifolia* are also common. These plants are low in stature (5 to 10 cm) and provide sparse cover (24%) (Bliss unpublished data).



FIGURE 3: View of Elk Mountain showing the south-facing slope, taken from the study area.

Plant Species Studied

Two species were chosen for detailed study. The first *Synthyris pinnatifida* var. *lanuginosa* was chosen because it is an important member of the ridgetop community which had not been killed by 1967 drought, and *Lupinus lepidus* var. *lobbii*, because it had been extensively killed, apparently by the drought.

Synthyris pinnatifida var. *lanuginosa* is an evergreen perennial, with fine, white, wooly hairs (Fig. 4). The plant lies close to the ground, ca. 3 to 5 cm high. The leaves are pinnately dissected with small ultimate segments. There is a rhizome from which long, and occasionally divided, roots extend for 10 to 20 cm. The raceme of purple-blue flowers is on a stalk above the leaves. Flowering occurs early in the season, April or May, following snow-melt. This variety of *Synthyris* is found only on rocky slopes at high altitudes in the Olympic Mountains (Hitchcock, *et al.* 1961).

Lupinus lepidus var. *lobbii* is a low, matted, evergreen, perennial, about 5 cm high, with upright greyish-green leaves (Fig. 5); the greyiness is due to abundant hairs on both leaf surfaces. The leaves are composed of five to nine leaflets. The raceme of blue flowers is borne on a stalk above the leaves. A taproot is present, frequently extending to bedrock (25 to 50 cm), and often trails up slope, reflecting the downslope movement of soils and stones. Flowering occurs in July and early August. *Lupinus lepidus* var. *lobbii* is found in the subalpine and alpine zones from British Columbia to southern California in the Cascade and Olympic Mountains (Hitchcock, *et al.* 1961).

Further discussion of general morphology is found in Results.



FIGURE 4: *Synthyris pinnatifida* var.
lanuginosa



FIGURE 5: *Lupinus lepidus* var. *lobbii*

METHODS

Microenvironment

Instruments were set up at the study site to obtain records of several environmental parameters. These instruments included a Belfort 3-cup anemometer placed at 60 cm, a Belfort hygrothermograph in a louvered shelter (Vogel and Johnson 1965) with the recording sensors between 10 and 25 cm, a Belfort pyranograph set on a horizontal platform on the ground and two Tru-chek rain gauges at 60 cm. This station was serviced once a week and checked several times during the day while investigations were being made.

An eight junction, millivolt, Grant recorder, programmed to print once an hour, measured temperatures. Sensors were placed at 10 and 5 cm over a clump of *Lupinus* at the surface under the leaves of the plant, and ca. -5 cm in the soil under the plant. Ten centimeters corresponds to flowering stalk height and 5 cm to leaf height.

Profiles of wind, temperature, and humidity were made over plants of *Lupinus* and *Synthyris* at various times during the summer, often with several readings during a day. Whenever possible paired profiles were made. Wind measurements were taken at 2, 5, 10, 20, and 60 cm with a Hastings thermopile anemometer using a directional probe. Readings at five second intervals were averaged from four or five profile replicates. Wet and dry bulb temperatures were measured with an electric psychrometer (Atkins) at the same positions. Temperatures were averaged over a five second period and recorded to the nearest 0.5°F. From these data vapor pressure

deficits were calculated.

Leaf temperatures were measured with a 36 gauge (0.127 mm) copper-constantan thermocouple and a Honeywell portable potentiometer. The thermocouple lead was placed under the leaf hairs to hold it against the under-surface of the leaf. If more support was needed, the insulated wire was held by hand several inches from the sensor. Ambient air was measured with the thermocouple, in most cases, at the time of leaf temperature reading.

Leaf Water Potentials

Relative water potentials of *Lupinus* and *Synthyris* were determined by a portable pressure chamber (Scholander, *et al.* 1965, 1966, Boyer 1967) to the nearest 1/3 bar. Two year old leaves, with direct exposure to sunlight, were chosen for measurement. Leaf temperature was measured prior to picking the leaf. The stem was wrapped with adhesive tape to prevent the petiole from being crushed under high pressure by the gasket and then sealed in the chamber. The time between picking and sealing the leaf was usually less than one minute. Once in the chamber, the petiole tip was cleanly cut near the end with a razor to determine more easily sap flow. During several periods throughout the summer, readings were taken, at least once (between 1100 and 1300 hr), and often several times a day, to obtain daily and seasonal patterns of leaf water potential.

Soils

Soil moisture was measured by gravimetric samples taken approximately once a week from depths of 10 to 15 cm and 20 to 25 cm.

The samples were oven-dried at 105°C for 24 hrs. From soil-moisture desorption curves, determined with 5 bar and 15 bar ceramic plant extractors (Soil Moisture Equipment Co. Catalogue 60), soil moisture was expressed in bars.

Textural analysis was made on the less than 2 mm soil fraction (Bouyoucos 1951, Reinhart 1961).

Morphological Studies

Approximately 20 plants, including roots, of *Lupinus* and *Synthyris* were carefully dug up. The general form of the rooting pattern and habit of the plants were noted. Root and shoot volume of several plants was determined by water displacement. Leaves of other plants were collected and pressed for determination of leaf area, using a leaf area meter with a photomultiplying tube. These leaves were then oven-dried at 105°C for 24 hr and weighed. The roots from the same plants were shaken free of soil and also oven-dried and weighed. From this information root-shoot ratios and other comparisons were made.

In 1970 leaves were gathered from five plants of each species and preserved in FAE. In the laboratory, 2 to 5 leaves from each plant were shaved and epidermal peels removed. The number of stomata/leaf area and the number of stomata/epidermal cells were counted under the light microscope. Except for one sample of *Lupinus* leaves, only the lower epidermal layer was examined.

RESULTS

Microenvironment

General Description

The study site on Elk Mountain has a rather harsh micro-environment due to the southern exposure and windward position. Three-day means for several microenvironmental parameters for the summer of 1969 are presented in Figure 6.

Solar radiation was greatest in July because of a longer day and a greater number of cloud-free days. The average radiation decreased from 580 ly/day in July to 455 ly/day in August to 382 ly/day in the first week of September. Maximum daily radiation recorded was 792 ly/day on July 22; maximum radiation of 1.6 ly/min was recorded on a partly cloudy July day. On a clear day typical values were ca. 650 ly/day compared to 325 ly/day on overcast days.

Winds tended to increase with the passing of summer, as did the incidence of stormy weather. During one storm in August, winds averaged 5.6 m/sec for a four day period. During this storm, winds were not measured for shorter periods, however, 1 cm copper tubing which has been standing upright was bent flat to the ground and instrument shelters which had been weighted with rocks were rolled over several times. For much of the rest of the season, winds were rather light (2 to 4 m/sec), coming from the southwest or occasionally from the southeast up the Badger Valley. On warm, clear days, small dust devils were observed.

Mean daily temperatures measured at 10 cm show a seasonal

FIGURE 6. Three-day means for several microenviromental parameters
for summer, 1969 Elk Mountain

A Solar Radiation

B Precipitation

C Soil Moisture

10 to 15 cm

20 to 25 cm _____

D Air Temperature (10 cm)

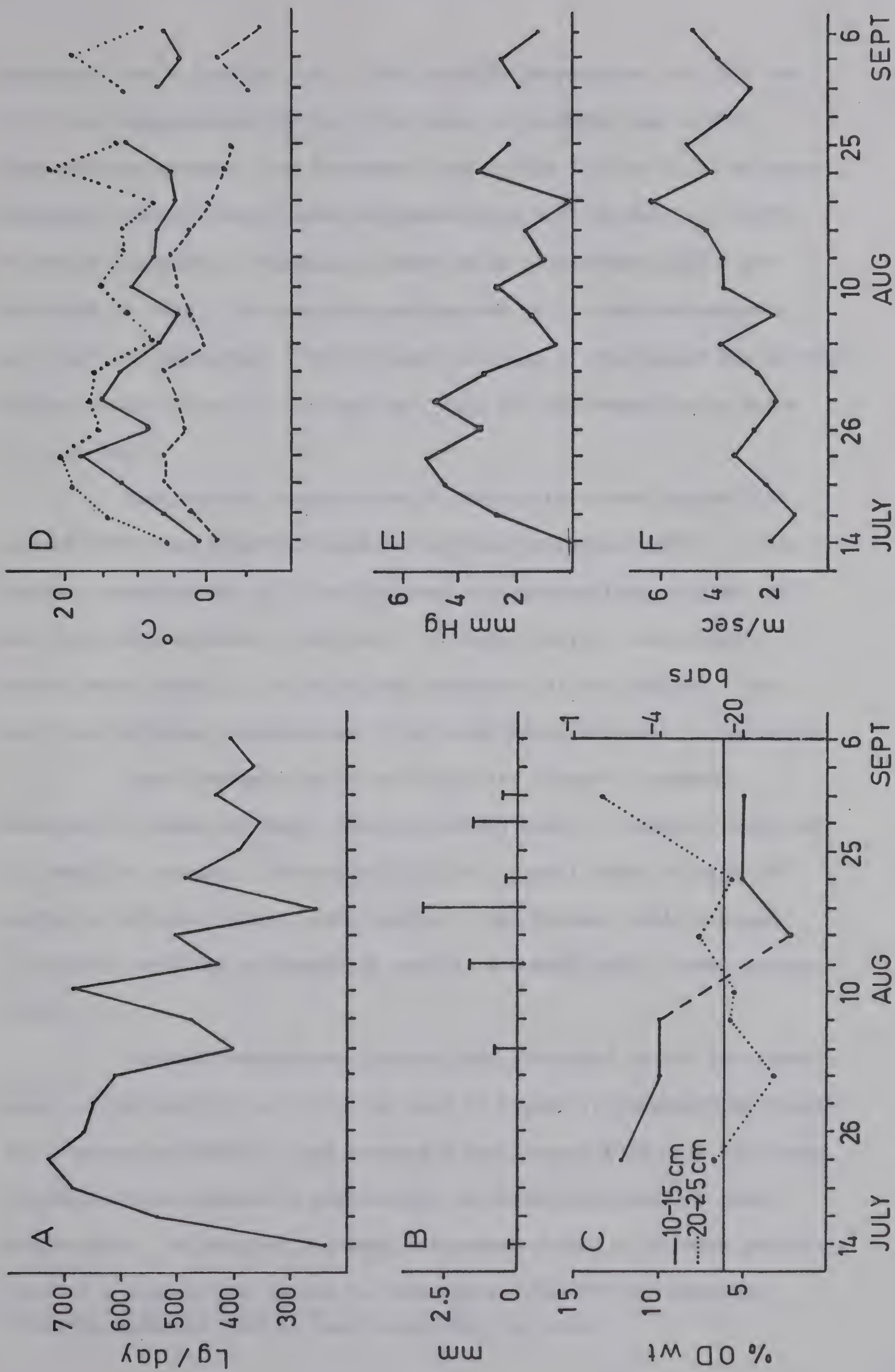
maximum

mean _____

minimum -----

E VPD (20 cm)

F Wind Speed (60 cm)



decrease from a peak in July. Mean monthly temperature for July was 10° ; mean temperature for the first week of September was 4.9°C . Maximum temperatures also decreased from 15° in July to 12.7° in August. Likewise minimum temperatures decreased from 3.3° in July to -4.8°C in early September. The highest mean daily temperature (22°C) was recorded in July. The absolute maximum was 26°C ; absolute minimum was -12°C in September. Thirty-eight per cent of the nights had minimum temperatures below 0°C , and one day, July 10, had temperatures below 0°C all day.

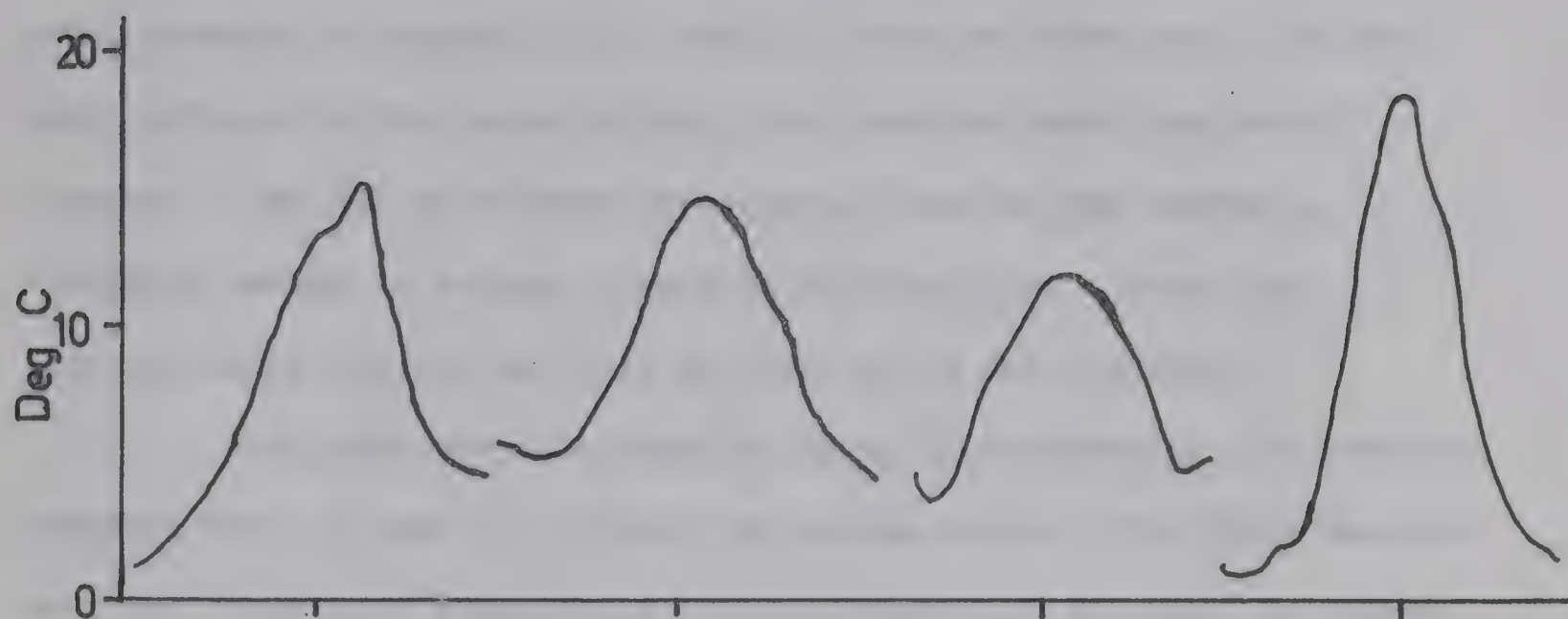
Mean monthly temperatures at the surface were highest in August (14°) and about the same in July and September (7.5°C). Mean monthly temperatures at -5 cm followed the same pattern, August, 12°C and July and September, 5.4° and 4.7° respectively. Mean monthly minima were below 0°C in August and September at the surface. The soil mean minimum temperatures (-5cm) were below 0°C only in September.

Vapor pressure deficits (VPD) also showed a seasonal decrease of about 0.7 mmHg . Average values were 2.7 mmHg for July and 2.0 mmHg for August. The end of July had several weeks of high VPD during a period of clear, warm weather. The highest daily average VPD's were recorded on August 22 and 23, 8.6 mmHg and 9.8 mmHg respectively.

Diurnal temperature fluctuations (measured in the instrument shelter) average 15° to 17°C . As seen in Figure 7, temperatures began to increase at 0600 hr*, and reached a peak around 1300 hr. VPD began to increase and reached a maximum two to three hours earlier than temperature. A range of 3.5 mmHg was common during a 24 hours period. Similar trends in the curves for temperature and VPD are expected

*Pacific Standard Time is used throughout the paper.

TEMPERATURE



V P D

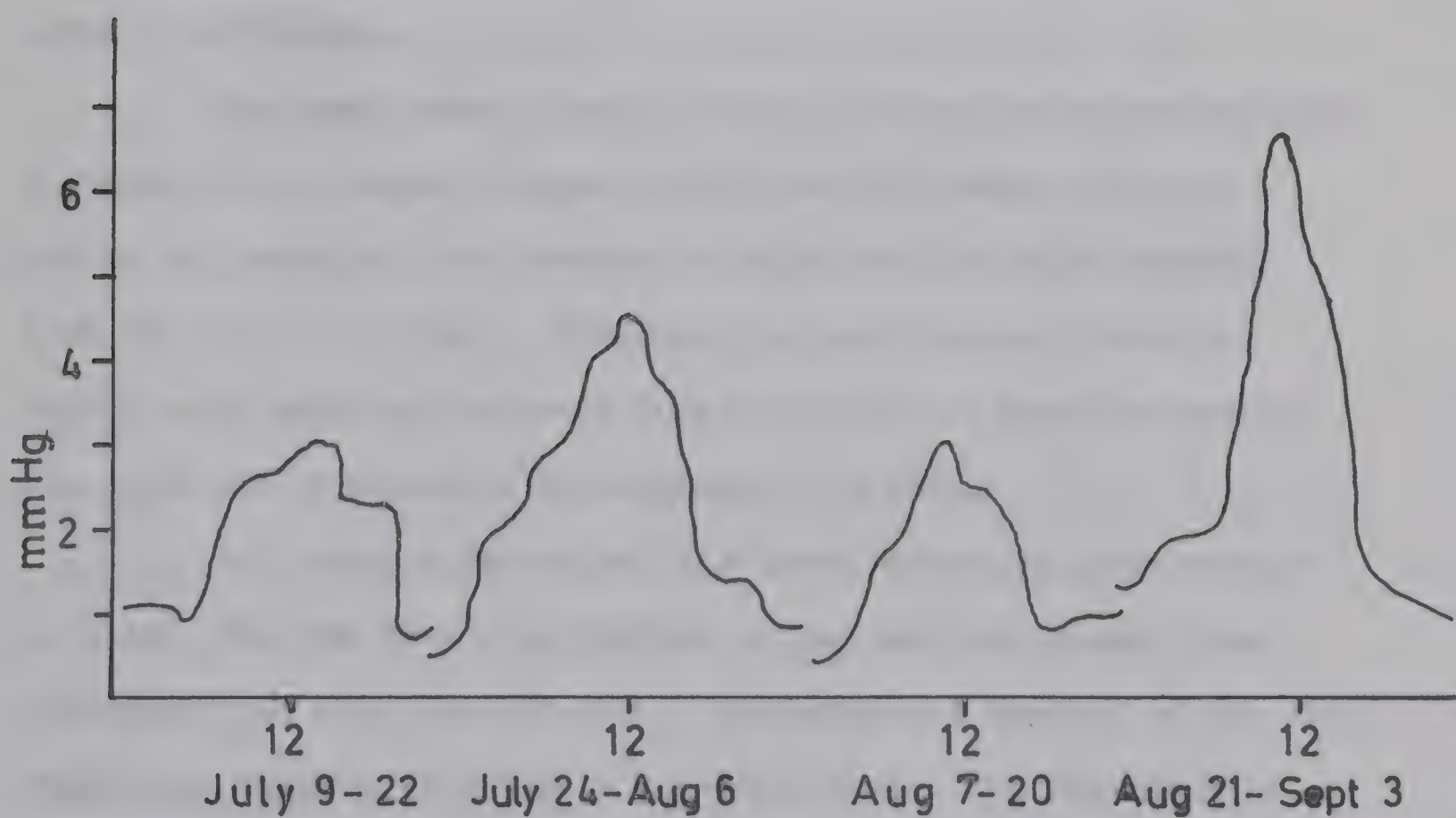


FIGURE 7. Diurnal temperatures and VPD regimes at 10 to 20 cm on Elk Mountain, Summer 1969. Hourly measurements are based on two-weekly means.

since VPD is a temperature dependent phenomenon.

Precipitation amounted to 24 mm for the ten week period. The greatest amount fell in early August. Most precipitation fell as rain, however, on August 5, 26, and 27, there was some snow. No data were gathered on the amount of dew, but numerous heavy dews were observed. Dew may be of some importance, since in one instance, *Synthyris* seemed to recover from mild wilting after a heavy dew, although other factors may well be involved in the recovery.

Soil moisture at a depth of 20 to 25 cm showed a slow seasonal decrease from -2 bars to -40 bars (by extrapolation). The first measurement was taken in a long period of fine weather of July 21. By August 11, soil moisture decreased to the summer low of -40 bars. For the rest of the summer, soil moisture increased only to -20 bars, despite rains in mid-August.

The upper layer of soil (10 to 15 cm) reflected precipitation patterns with a gradual increase in moisture following each rain. During the period of clear weather in July, soil moisture dropped from -10 bars to -21 bars. Following the more frequent rains in August, soil moisture increased from -14 bars to -8 bars for much of the month and by September 1, increased to -2 bars.

Soil texture determines to a great extent how much moisture is held. The less than 2 mm fraction of the soil was a sandy loam (70% sand, 12% clay, and 18% silt). Approximately one-half of the soil weight was composed of stone in the upper 10 cm. The proportion of stones increased with depth (67%).

Comparison with Previous Years

Summaries of microenvironmental data from 1965, 1966

(Bliss 1969), and 1969 and estimates from 1967 are given in Table 1. The 1965 and 1966 data are from a meadow ca. 100 m to the northwest and ca. 20 m lower in elevation in a slightly more sheltered site than the ridge of Elk Mountain. The comparison shows July 1969 was sunnier, with less wind and higher VPD than the combined July average in 1965 and 1966. Precipitation was also lower in 1969. August 1969 was sunnier, but cooler (ca. 2°C). VPD and precipitation were lower than in 1965 and 1966. The lower temperature and VPD in August 1969 may have compensated for the dryness earlier in the summer and during that month.

In a dry, subalpine meadow between Hurricane Ridge and Elk Mountain, Kuramoto (1968) maintained an environmental station in the summers of 1966 and 1967. This station is 200 m lower in elevation than the Elk Mountain ridge, with an open grass-forb community and a southerly exposure. Since solar radiation, temperature and VPD seem to be higher here than in the Elk Mountain alpine, only limited use of the data may be made. The 1967 alpine estimates are based on extrapolation from the 1967 subalpine data, using the 1966 data from the two sites as a basis for calculation. The results are presented in Table 1. It would seem that August was very dry and warm, exceeding any of the other three years. This is also supported by a VPD three-day mean in late August of 13 mmHg. The lowest VPD mean for the month of August, in the subalpine zone, was 4 mmHg. Early in September 1967 the dry period was ended with 4 cm of rain. While this summer was not the driest, it probably resulted in the most stress for the vegetation.

Table 1. Comparison of microenvironmental data for four summers. The 1965-1966 data are the monthly averages for the two year period (Bliss 1969). The 1967 data are estimates based on 1967 data from the subalpine zone (Kuramoto 1968).

Month/year	Solar Radiation ly/day	Temperature °C	Wind 60 cm (m/sec)	VPD (mmHg)	Precipitation (cm)
JULY					
1965	595	10.6	3.4	3.2	1.8
1966	477	8.3	3.0	2.3	3.2
1967*	550	9.0	---	---	0.3
1969	580	10.0	2.2	2.7	0.02
AUGUST					
1965	388	8.3	4.5	3.0	5.0
1966	478	9.8	3.1	4.0	1.5
1967*	450	12.0	---	---	T**
1969	455	6.9	3.8	2.0	2.1

* estimated
 **T = Trace

Comparison with Another Station

The nearest permanent weather station is in Port Angeles, to the north and situated near sea level. Comparisons of the 1969 temperature records from Port Angeles (5 m) and Elk Mountain (1972 m) do not show much correlation due to altitudinal differences and method of obtaining data. Temperatures recorded in Port Angeles have a mean monthly value 10 to 17°C higher (a difference of 11°C might be expected due to lapse rate) during July, August, and September. These temperatures in Port Angeles are near normal for the time of year. Mean maximum temperatures were about 5.5° higher and mean minimum temperatures about 11°C higher in the town than on Elk Mountain. Precipitation records were more nearly in agreement; both areas lie in the rain shadow of the central Olympic Mountains, and especially in summer have similar major precipitation patterns. Table 2 presents mean monthly precipitation and temperatures for Port Angeles (U.S. Dept. of Commerce Climatological Data, 1966) and Elk Mountain.

The Port Angeles record is of value for determining how closely the weather agrees with the long term normal for the area. In 1969 the summer was near normal. During 1967, the year of the drought, Phillips (1967) reported in July that the weather for western Washington was warmer than average and that precipitation had been low since the first of April. The weather was especially hot and dry in the Olympic Peninsula. At end of July, Phillips stated, "the last beneficial precipitation was recorded on June 21 and 22." Records for August in Port Angeles (U.S. Dept. of Commerce Climatological Data 1967) show 1.45 cm precipitation, 2.85 cm less than the normal and temperatures 2°C higher. It can be expected that the alpine area on

Elk Mountain was unusually dry and warm, indicated in the estimated values in Table 1.

Table 2. Comparison of mean monthly temperatures and precipitation for Port Angeles (PA) and Elk Mountain (EM) for the summer of 1969. Deviation from normal is indicated in Port Angeles data.

Month	Site	Mean (°C)	Mean Max (°C)	Mean Min (°C)	Ppt (cm)	
July *	PA	15.6	(+0.7)	19.8	11.4	0.8 (-0.5)
	EM	10.0		13.4	1.1	0.03
Aug.	PA	15.2	(+0.4)	19.3	11.1	1.5 (+0.07)
	EM	5.4		12.5	1.4	2.1
Sept.**	PA	15.0		20.0	11.7	0.4
	EM	-0.3		15.0	-3.9	0.0

* July 7 to 31

** September 1 to 7 only

Environmental Profiles

Continuous Temperature Profile for *Lupinus*

The temperature environment of *Lupinus* was monitored throughout the summer at the 4 levels described in Methods. The profiles gave different information from temperature measurements in the shelter (Fig. 8). On a cloudy day, shelter temperature was lower by several degrees than temperature near the plant; on clear days shelter temperature was more nearly in line with plant temperatures, but was higher than the 10 cm level over the plant. These differences were due to the less responsive hygrothermograph sensors and the reduced air circulation within the shelter.

Soil temperature (-5 cm) was usually within 1 to 2°C of the surface temperature (0 cm). This was most likely due to the stony nature of the soil which would enhance heat conductivity. For a 24 hour period, the average temperature at 10 cm was the highest of the four levels monitored. However, the maximum and minimum temperatures were recorded at the 5 cm level (Fig. 9) which is at the plant surface. The leaves create the surface which experiences the greatest heat load; the ground is protected by the plant. On clear nights slight temperature inversions occurred at the plant surface. The heat load decreased slightly during the course of the summer, eg. $\Delta T = 53^{\circ}\text{C}$ on July 19, $\Delta T = 40^{\circ}\text{C}$ on Sept. 1 (Fig. 9).

Short Term Profiles

Especially during July, spot profiles were made over *Lupinus* and *Synthyris* clumps to describe the immediate environment of the plants

FIGURE 8. Daily temperature profile for *Lupinus* on a cloudy and a clear day. Air temperature from shelter is included.

10 cm -----

5 cm

0 cm -.-.-.-.

-5 cm -...-...-...

Shelter temperature (10 cm) _____

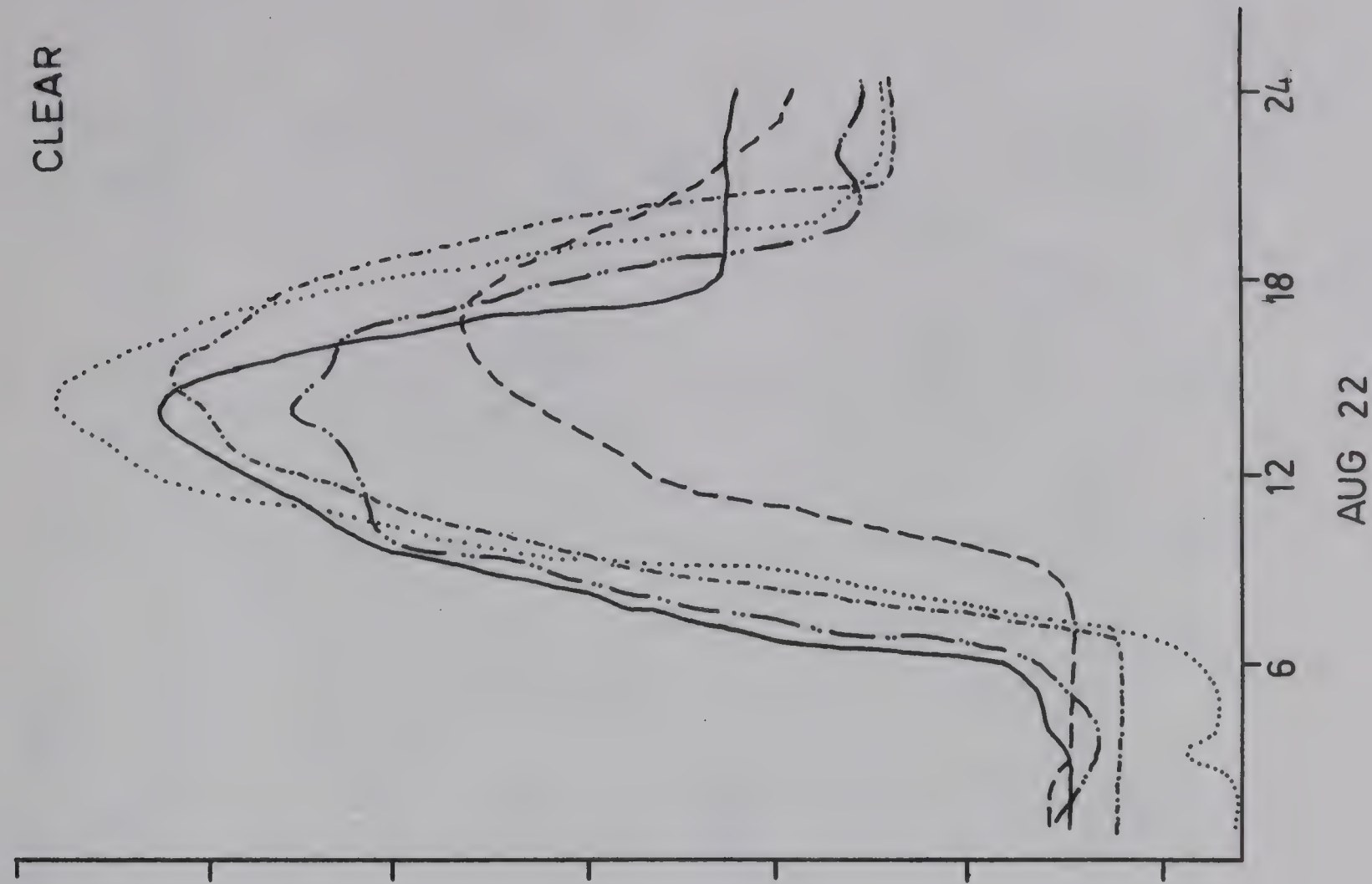
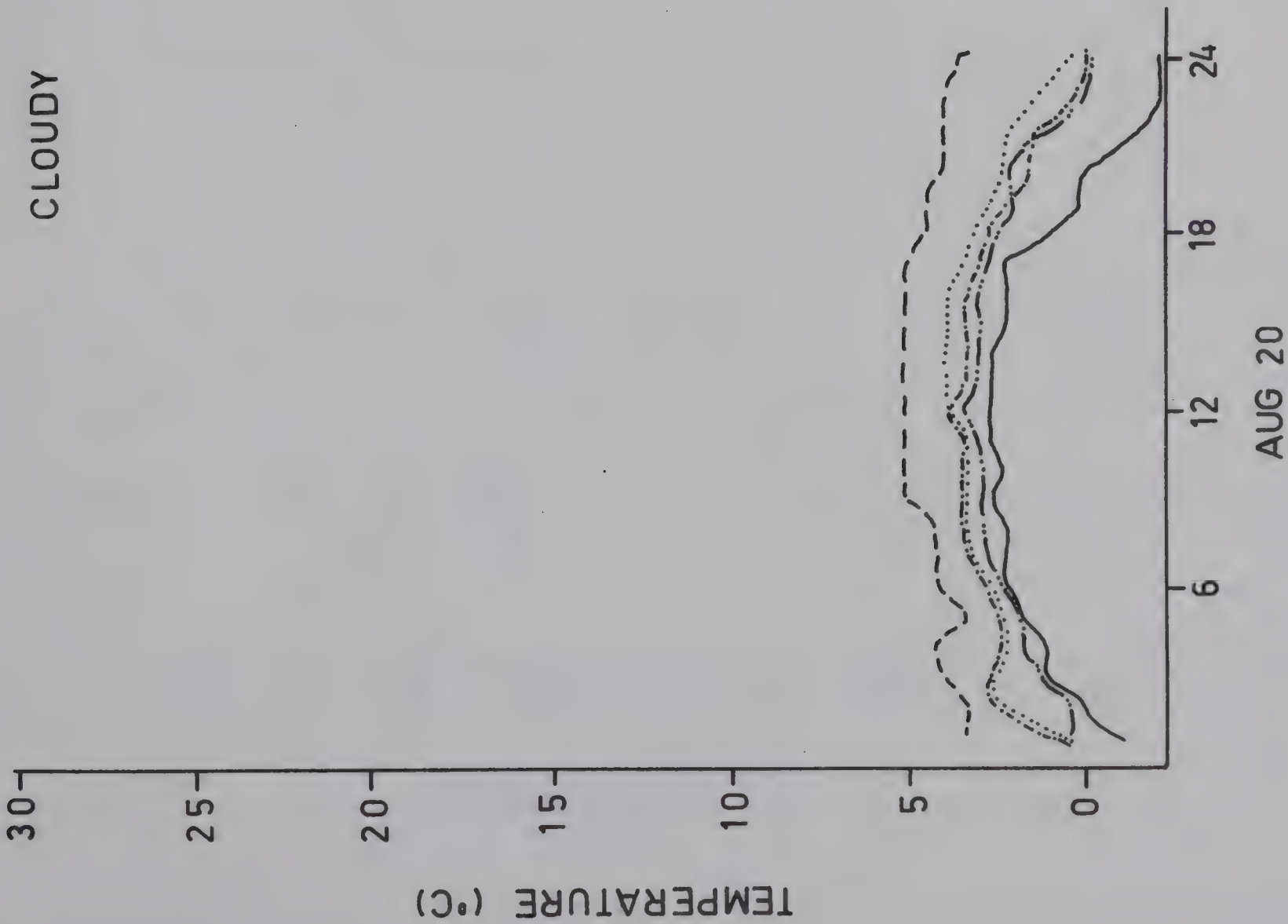
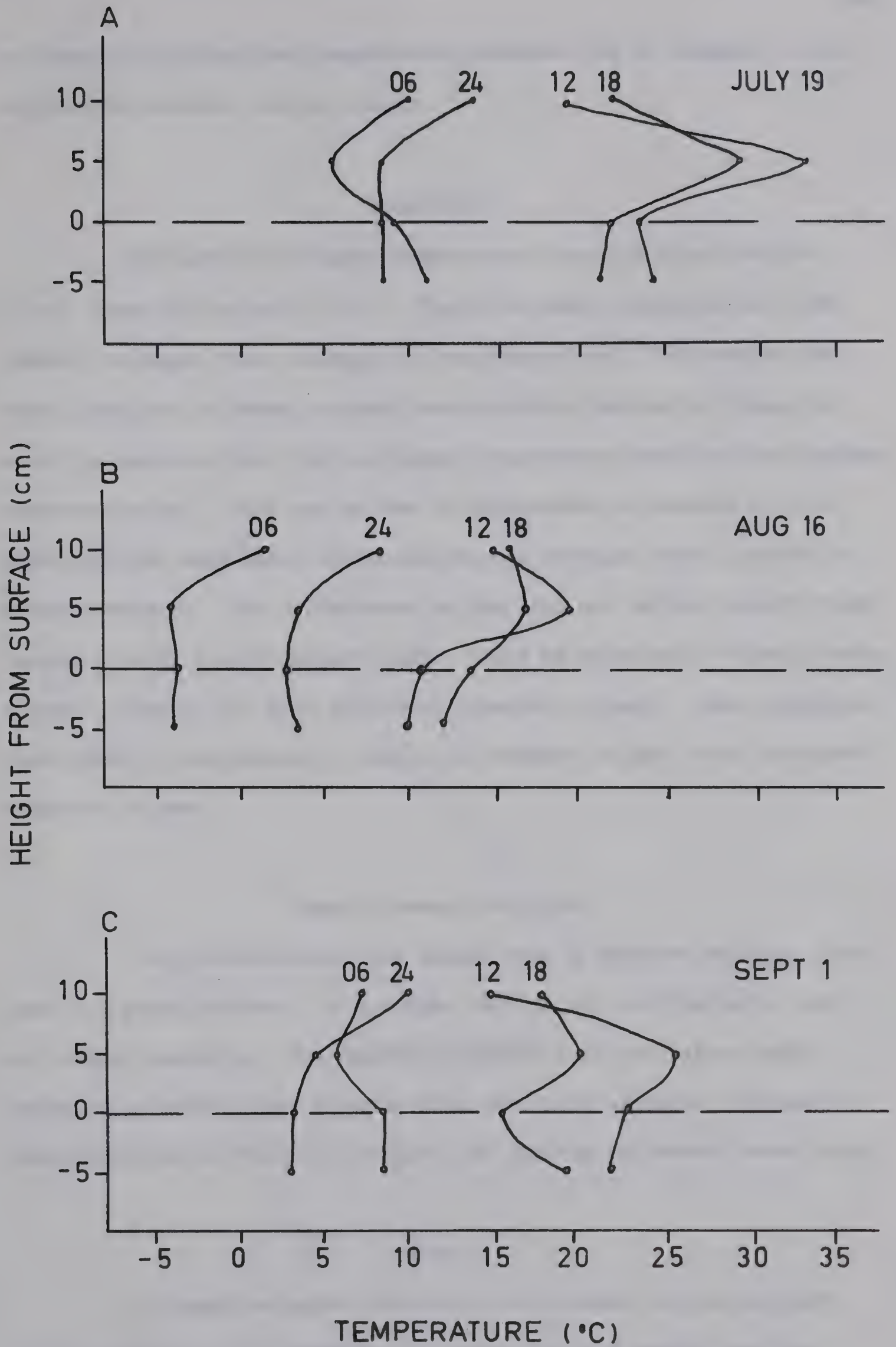


FIGURE 9. Seasonal trend of daily temperature profiles for *Lupinus*.



in terms of moisture and temperature gradients and in attempt to find differences between the two plants.

Temperature

Synthyris had higher temperatures over the plant surface (2 cm) than did *Lupinus* (5 cm). Figure 10 shows a profile for both plants, averaged from readings of four sunny days. The heating just over *Synthyris* is shown; no such heating above *Lupinus* is found, as would be expected from the continuous temperature profiles from *Lupinus* mentioned above. This may be due to differences in sensors or that spot profiles were taken in succession and averaged over a period of several seconds. The differences in profiles may reflect growth forms. *Lupinus*, being a more upright plant, would be affected by winds blowing across, allowing for more efficient transfer of heat. Since *Synthyris* lies close to the ground, it would not benefit so much from turbulent transfer of heat.

Vapor Pressure Deficits

The profiles over both plants show a negative moisture flux near the plant surface. At a height over 20 cm the flux may or may not remain negative. The moisture gradient over the plants would indicate potential loss of water from the plant surfaces. Figure 11 shows profiles of VPD for *Synthyris* and *Lupinus* on several sunny days.

Wind

In many instances the wind profiles over the two species do not conform to the standard "J" curve for wind speeds near the

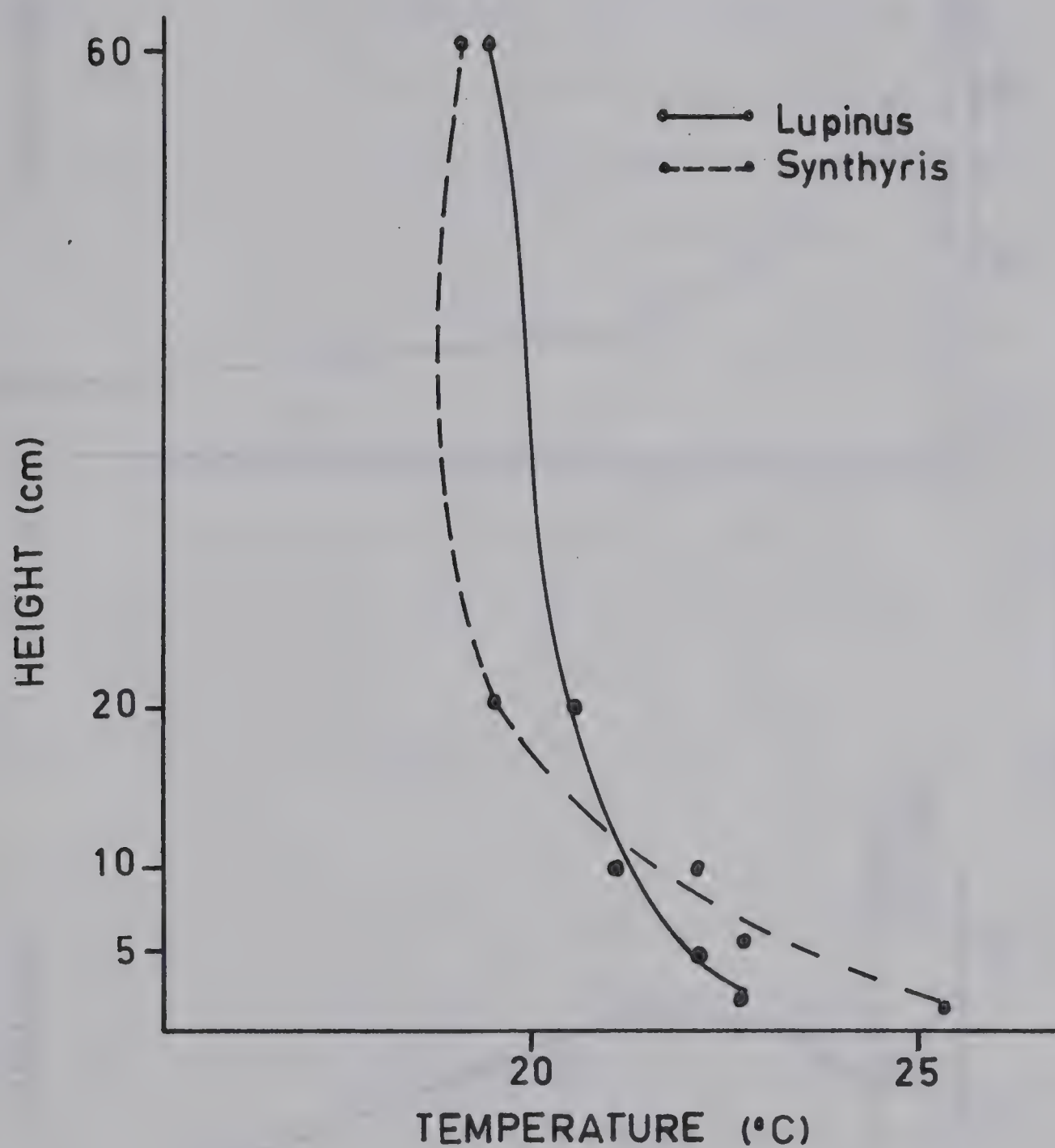


FIGURE 10. Temperature profiles for *Synthyris* and *Lupinus*. Curves are based on average of four sunny days.

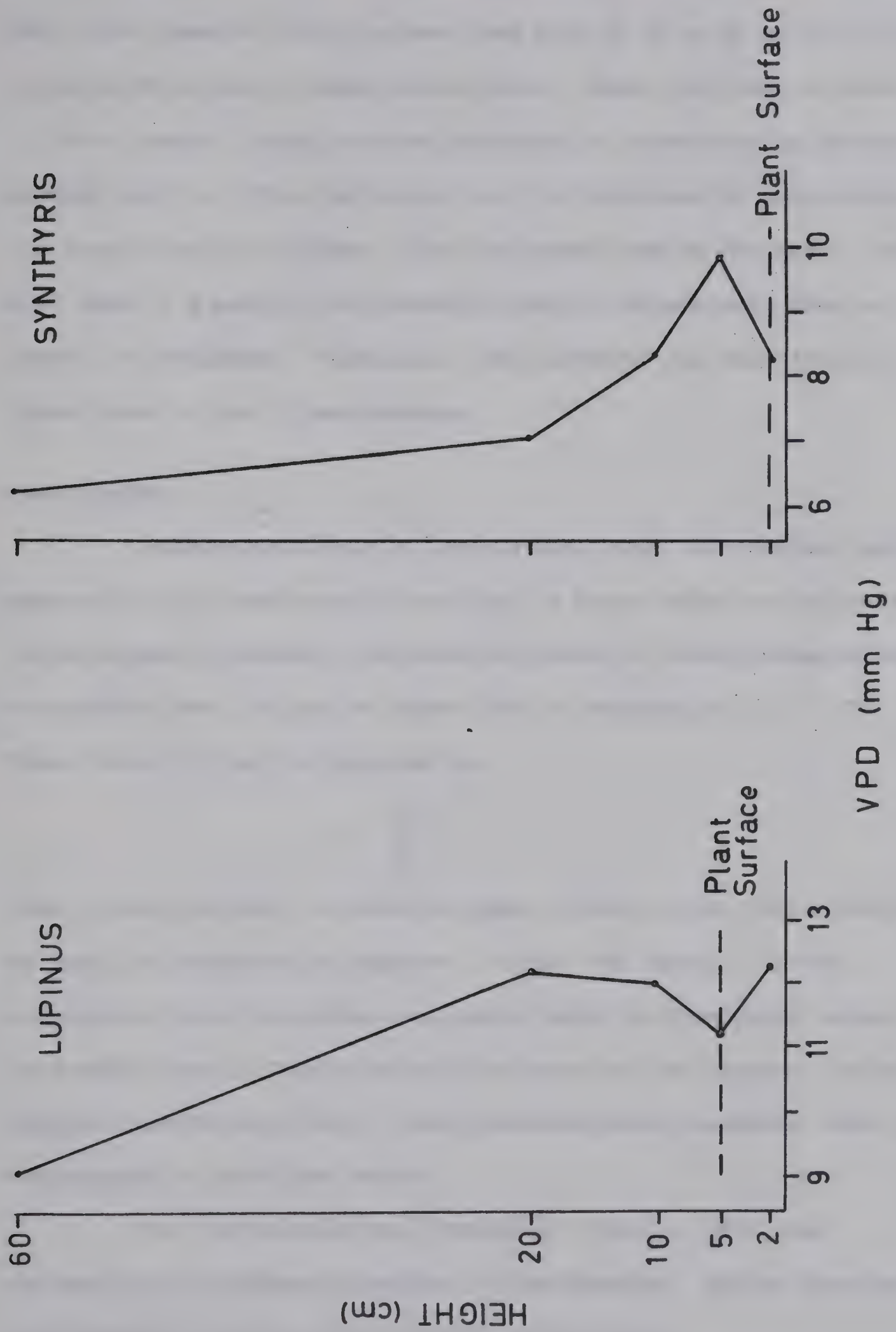


FIGURE 11. VPD profiles for *Lupinus* and *Synthyrus*

ground (Fig 12C). This is especially common in the case of *Lupinus*, where wind speed at 60 cm is less than that at 20 or 10 cm (Fig. 12A) in one-half of the 37 measurements taken. Since the plant is erect, it would create a rough surface, resulting in turbulence in the winds passing over it. This turbulence would be important in maintaining the heat balance in *Lupinus*. The low growth form of *Synthyris*, which must make it a part of the boundary layer of the surface, does not create the roughness. Turbulence over *Synthyris* was recorded only three times in the 37 measurements.

Bowen Ratios

Because gradients in temperature, wind, and moisture were measured in the environmental profiles, a Bowen ratio was calculated in an attempt to estimate the relative amount of energy being dissipated as sensible heat (H) and as latent heat of evaporation (LE). The Bowen ratio (β) may be expressed as:

$$\beta = \frac{H}{LE}$$

From a moist surface, LE would be great, giving a ratio which should be small or occasionally negative. From a dry surface, little evaporation could take place and energy would be dissipated largely as sensible heat. The ratio would be large and may approach infinity (Slatyer and McIlroy 1961). Plant surfaces which transpire freely may be expected to yield low ratios.

For the calculation, Fritschen's formula (1965) was adjusted for the higher elevation of the Olympics. Values from the environmental profiles at 20 and 60 cm were used.

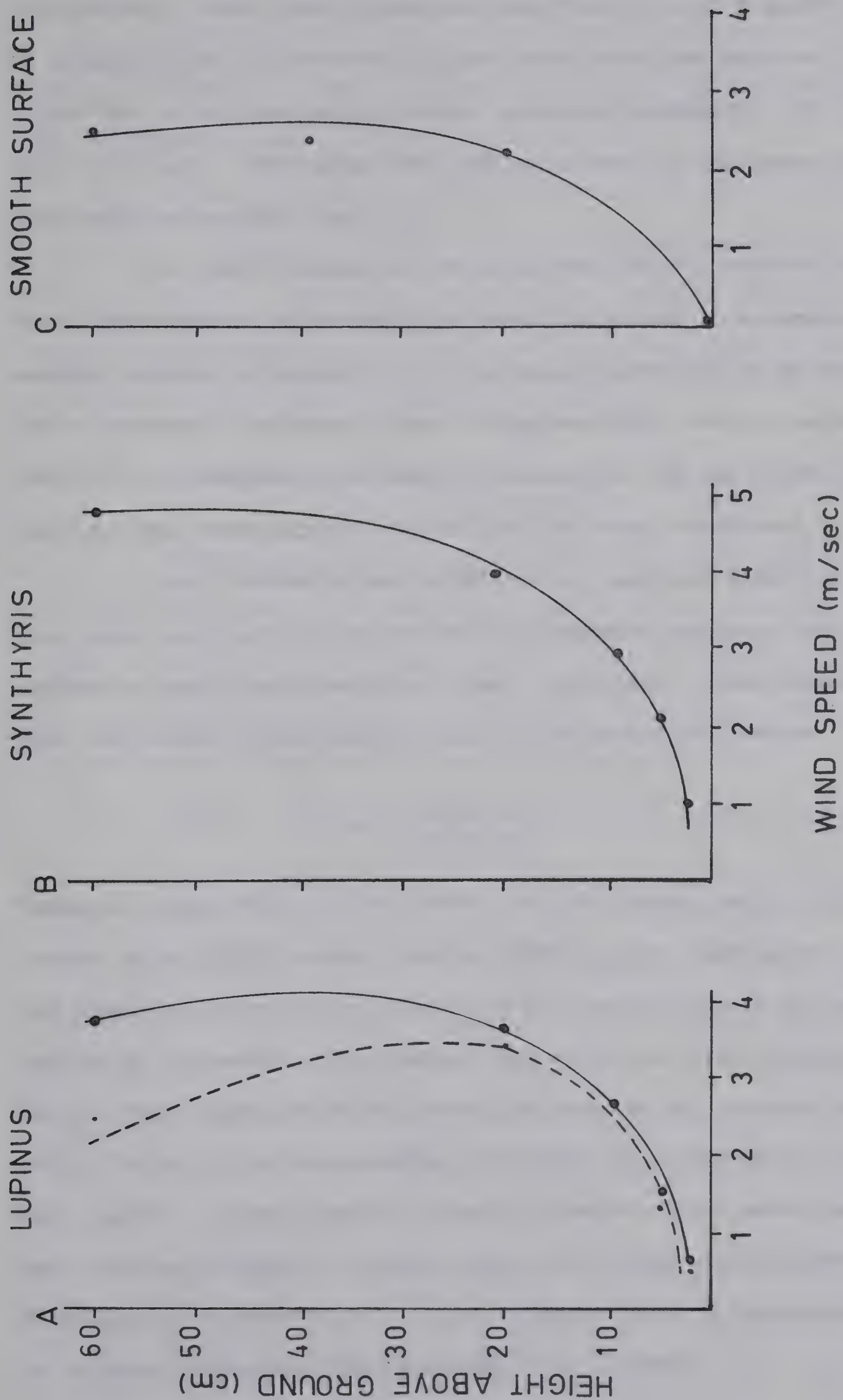
No statistical difference was found in the values for the

FIGURE 12 A. Wind profile for *Lupinus*.

_____ average of 37 readings in July
----- average of only those readings
(19 of 37) which showed turbulence.

FIGURE 12B. Wind profile for *Synthyris*. Curve is average of 37 readings in July.

FIGURE 12C. Wind profile over a smooth surface (from Halstead and Covey 1957).



two species. Since plant clumps are less than 25 cm in diameter, it is unlikely plant differences, if any, could have been measured, but rather the values obtained represent the entire community. The values of β were high, averaging 2300, indicating most of the energy was dissipated as sensible heat (H).

The high β values must be used with caution, because the Atkins psychrometer is probably not sensitive enough to accurately measure moisture as needed (1/3 of the measurements had to be discarded due to improbable moisture fluxes [Fritschen 1965]) and the surface cover is not homogeneous as usually required for the use of the Bowen ratio so that advection may account for the large H indicated.

Spot readings of net radiation (R_n) and soil heat flux (S) were taken one clear day at noon with a Fritschen miniature net radiometer and a Thornthwaite soil heat flux plate. These values plus the average β were used to find LE (Fritschen 1965) where

$$LE = \frac{-R_n + S}{1 + \beta}.$$

Measured values of $R_n = 0.75$ ly/min, $S = 0.26$ ly/min, and $\beta = 2,300$ yielded $LE = 0.0058$ ly/min. Courtin (1968), on Mt. Washington in New Hampshire, obtained an LE value of 0.15 to 0.25 ly/min for two species in lysimeters. He observed that water was rarely limiting. In the White Mountains in California, Terjung, *et al.* reported LE to be 0.7 ly/min by the Bowen method. The White Mountains have a drier, more rigorous climate than the Olympics, however, their measurements were made on the edge of a small lake so that water would be less limiting for the vegetation. In an irrigated field (a non-alpine site) in Arizona, Fritschen (1965) measured LE as 1 ly/min.

On Elk Mountain, water may be limiting at times, and therefore lower LE values than reported elsewhere might be expected, but probably not as low as indicated by the calculations.

The heat load of the leaves (ΔT 's of 5 to 10°C, see below) and the low soil moisture levels (-10 to -20 bars) support the finding of low LE values. Readings nearer the plant level (5 and 10 cm) rather than at a higher position (20 and 60 cm) might result in a better estimate of the LE over a vegetated surface.

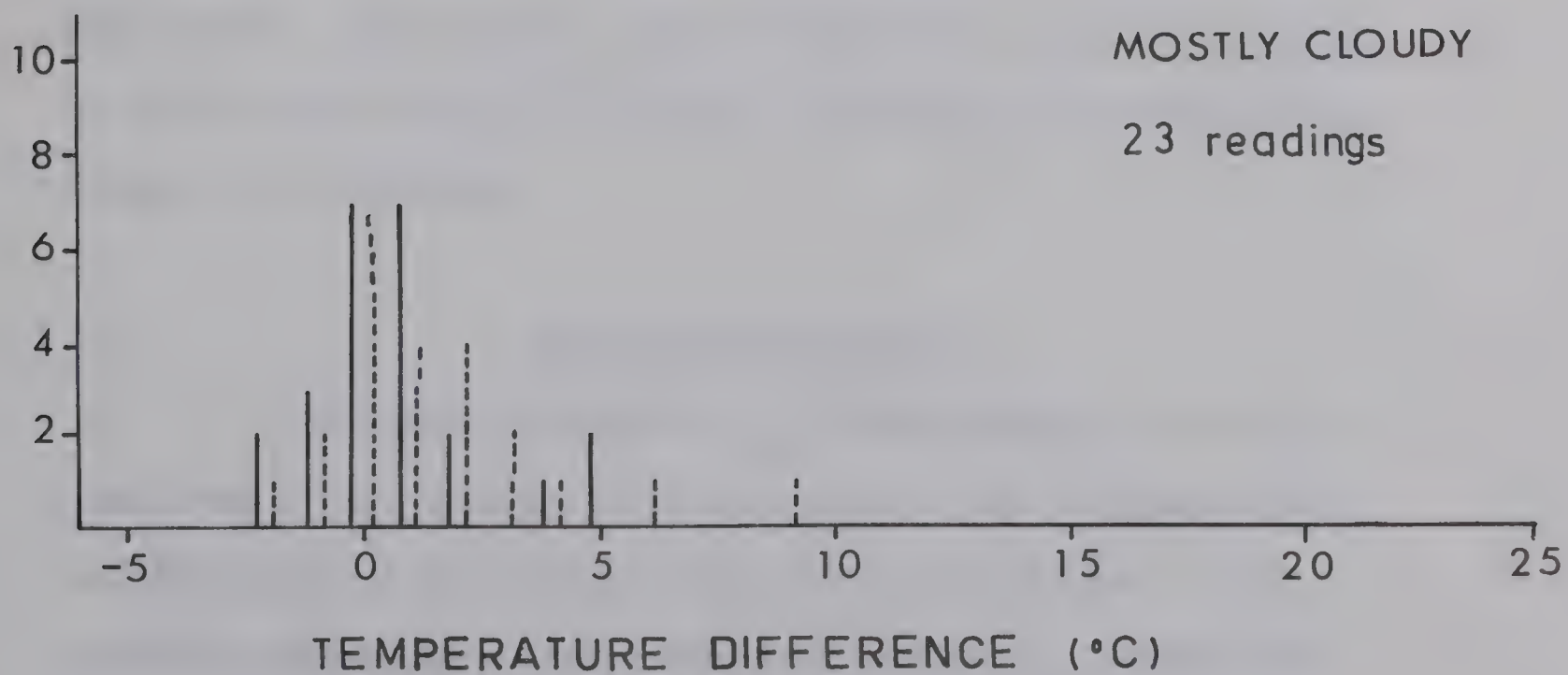
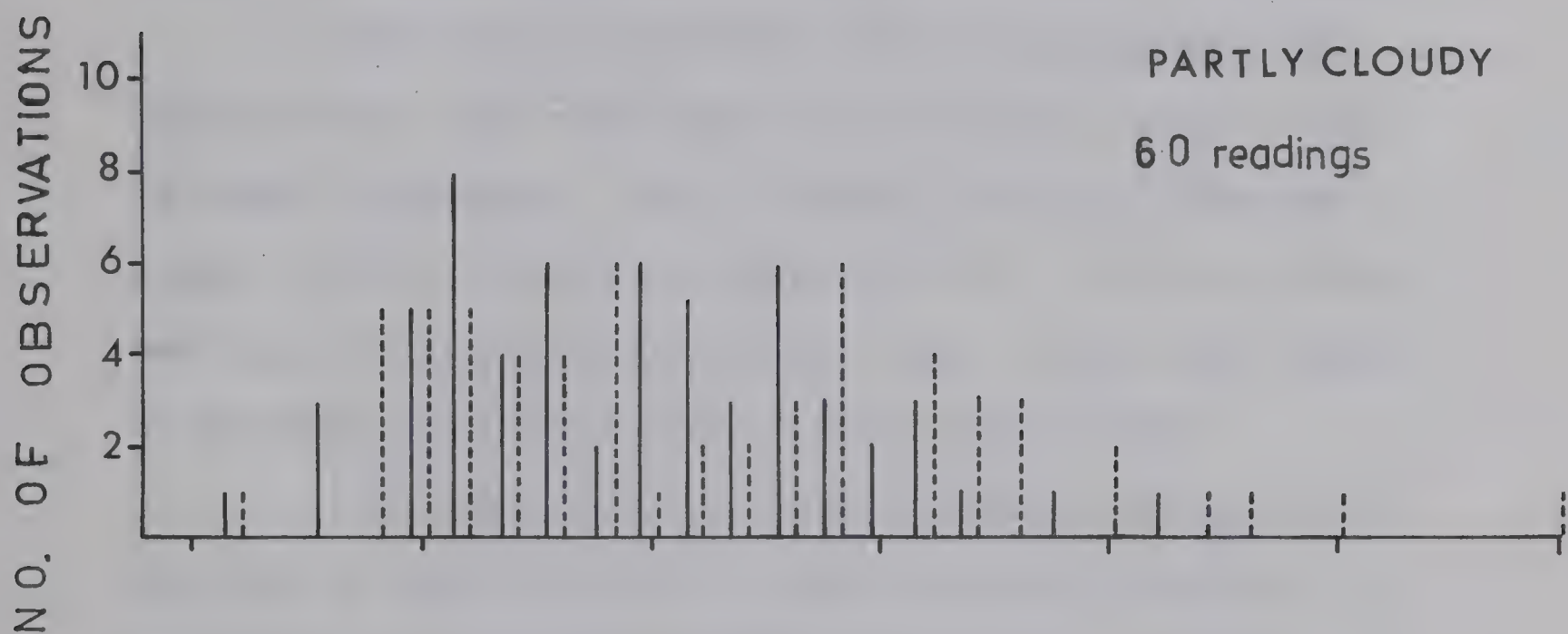
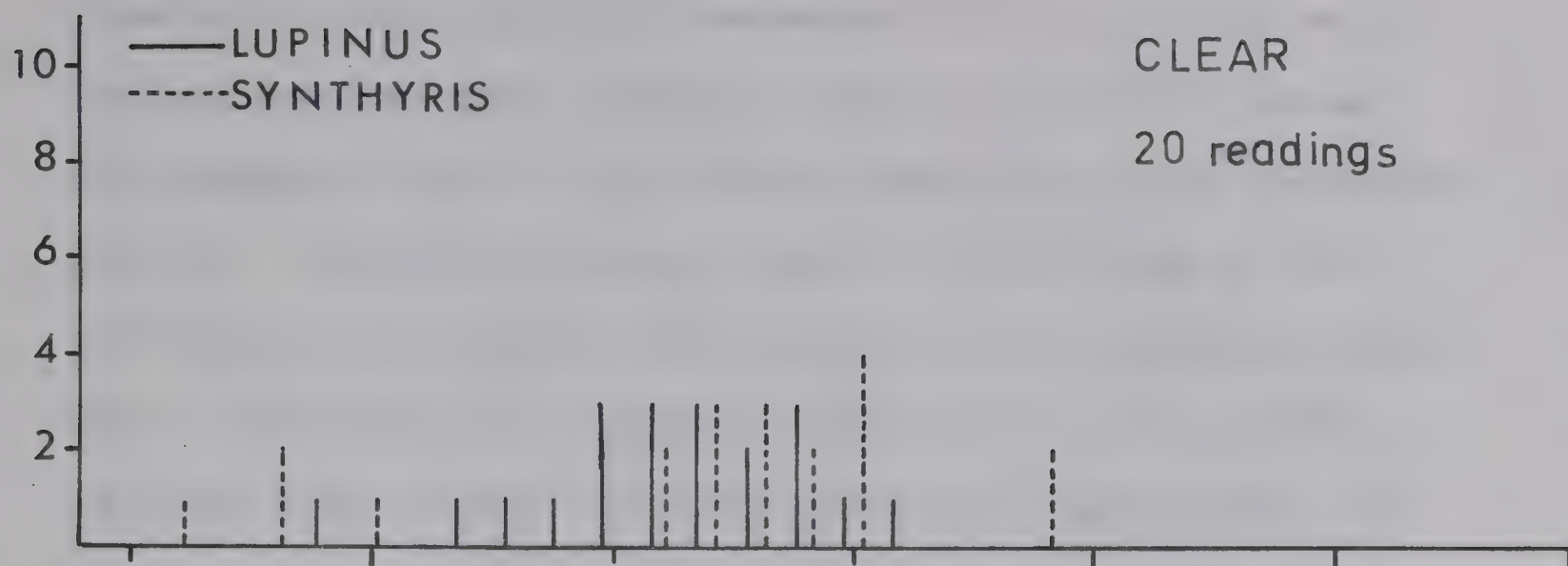
Leaf Temperatures

Temperatures, which are important to physiological processes, increase in leaves by the inability of the plant to completely dissipate radiation received. In alpine areas radiation is high because of the less efficient screening of the thinner atmosphere. This often results in leaf temperatures greater than ambient.

Warren Wilson (1957) and Courtin (1968) report a correlation of wind speed and leaf temperature. Higher wind speeds reduce heating of the leaf by reducing the boundary layer of leaves and other plant parts and increasing turbulent transfer of heat from plant surfaces. While such a correlation was expected from data gathered in the Olympics, none was found. The lack of correlation may be due to the generally light winds which prevail and in the case of *Synthyris*, the low growth form of the plant. Leaf temperature would seem to be more related to cloud cover and hence radiation (Fig. 13).

Differences in leaf temperature between the two species were found. *Synthyris* had the greater range of leaf temperatures and greater average deviations from ambient air temperature (Fig. 9). The greatest

FIGURE 13. Departure of leaf temperature from ambient air temperature on clear, partly cloudy and cloudy days.



departure of leaf temperature from ambient (ΔT) was recorded on a partly cloudy day, when a *Synthyris* leaf had a ΔT of 25°C ; actual leaf temperature was 36° , rock surfaces were 40° , and air temperature was 11°C . On several occasions, negative ΔT 's (as large as -4°C) were recorded from leaves of both species on clear and partly cloudy days. The average ΔT of *Synthyris* leaves was $+9^{\circ}$, $+8^{\circ}$, and $+3^{\circ}\text{C}$ on clear, partly cloudy, and mostly cloudy days respectively. For *Lupinus* leaves, the ΔT 's were lower ($+6.5^{\circ}$, $+5.5^{\circ}$, and $+2^{\circ}\text{C}$ respectively). The values of ΔT increased with the advance of the season.

Twenty-five, paired leaf temperature measurements with replicates were taken from *Lupinus* and *Synthyris* at various times in August and September. In 14 instances, *Synthyris* leaves had a higher ΔT than *Lupinus* by an average of 3.2°C . In 6 cases, *Lupinus* had higher ΔT 's, but were an average of only 2° warmer than leaves of *Synthyris*. On five occasions the ΔT 's were the same.

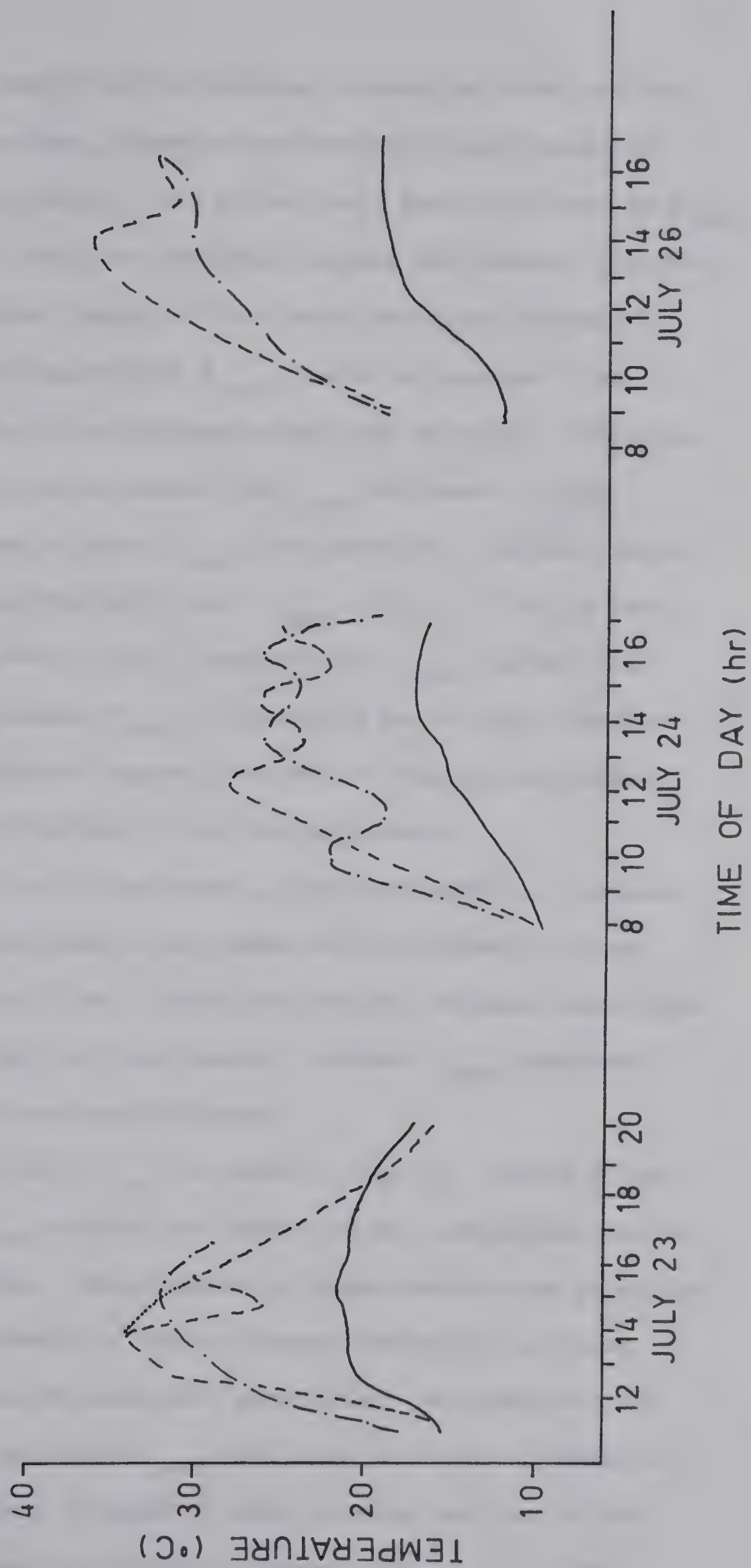
Leaf temperatures were highest during mid-day and early afternoon as seen in Fig. 14, the time of greatest insolation. In most cases leaf temperatures exceed air temperatures measured in the shelter. Fluctuations in leaf temperatures occur with shading as can be seen in Fig. 14, July 24, a day when intermittent clouds formed in the afternoon.

Leaf Water Potentials

Leaf water potentials (Ψ_{leaf}) were measured to serve as indicators of the relative moisture status of the two species and the efficiency of the plants to obtain or conserve water. The pressure chamber was used to estimate relative Ψ_{leaf} (Boyer 1967).

FIGURE 14. Comparison of leaf temperature of *Synthyris* and *Lupinus* with air temperature, measured in the instrument shelter at 10 cm, on three days. July 24 experienced intermittent cloud; the other two days were sunny.

Synthyris -----
Lupinus -.-.-.-
Air _____



No corrections for temperature differences between the plant and the pressure chamber were made, since errors from this source would be less than the reading error. Also as much as 3 bars difference in Ψ_{leaf} could be measured on one plant depending on age, and probably position, of the leaf. A narrower range of 1 bar was a more usual situation.

The seasonal pattern of Ψ_{leaf} of the two species (Fig. 15) is fairly well related to precipitation and soil moisture. Following rains, when soil moisture increased the Ψ_{leaf} increased. Until September, *Lupinus* had a higher Ψ_{leaf} than *Synthyris*. *Lupinus* rarely exceeded -23 bars, and typically had a Ψ_{leaf} of ca. -12 to -14 bars. During a very dry period of July, *Synthyris* had Ψ_{leaf} values lower than -27 bars. The average Ψ_{leaf} of *Synthyris* was -21 bars for the summer. These differences suggest that the two species are differently adapted for utilization of the available water.

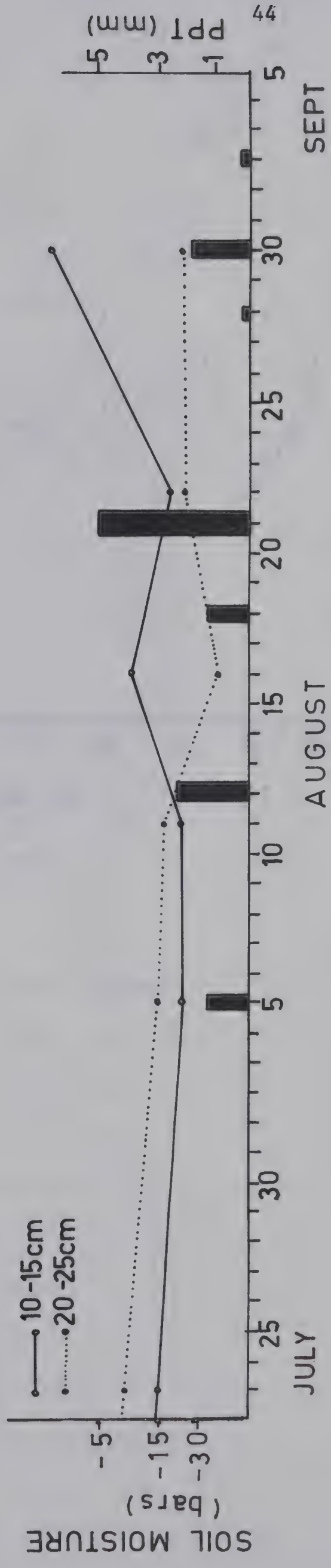
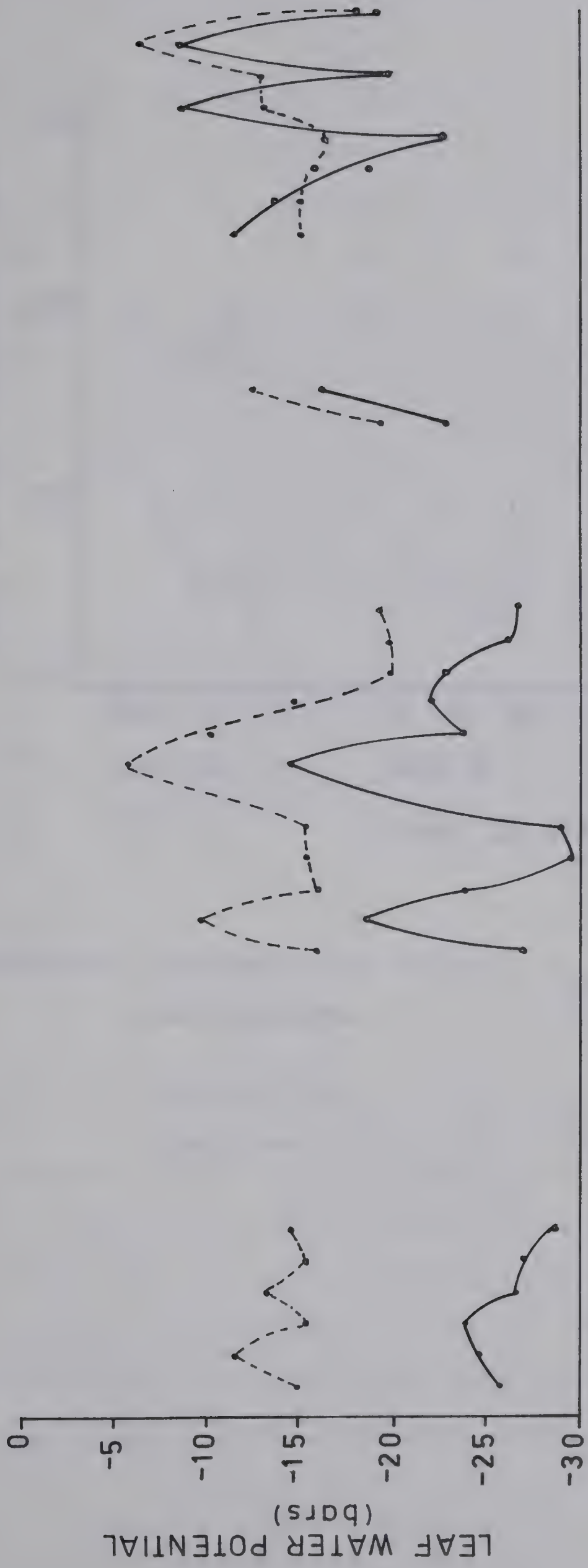
Toward the end of the season, *Synthyris* showed an increase in Ψ_{leaf} , which corresponded to increased soil moistures (-2 bars) at upper levels (10 to 15 cm). *Synthyris* probably obtained water from this portion of the soil in late summer. *Lupinus'* Ψ_{leaf} remained relatively constant throughout the summer.

Daily pattern of Ψ_{leaf} is shown in Fig. 16. During midday (1100 to 1300 hr) Ψ_{leaf} reached the lowest values, undoubtedly due to increased transpiration. Measurements of transpiration were attempted with hydrostatic lysimeters. Due to frequent mechanical problems in the field, the data obtained were unreliable, and therefore, not included. Recovery to higher Ψ_{leaf} took place at night as indicated by the higher potentials obtained in early morning and late afternoon. *Synthyris* showed greater daily ranges of Ψ_{leaf} , up to 10

FIGURE 15. Seasonal trend of leaf water potential of *Synthyris* and *Lupinus*, and soil moisture.

Synthyris _____

Lupinus -----



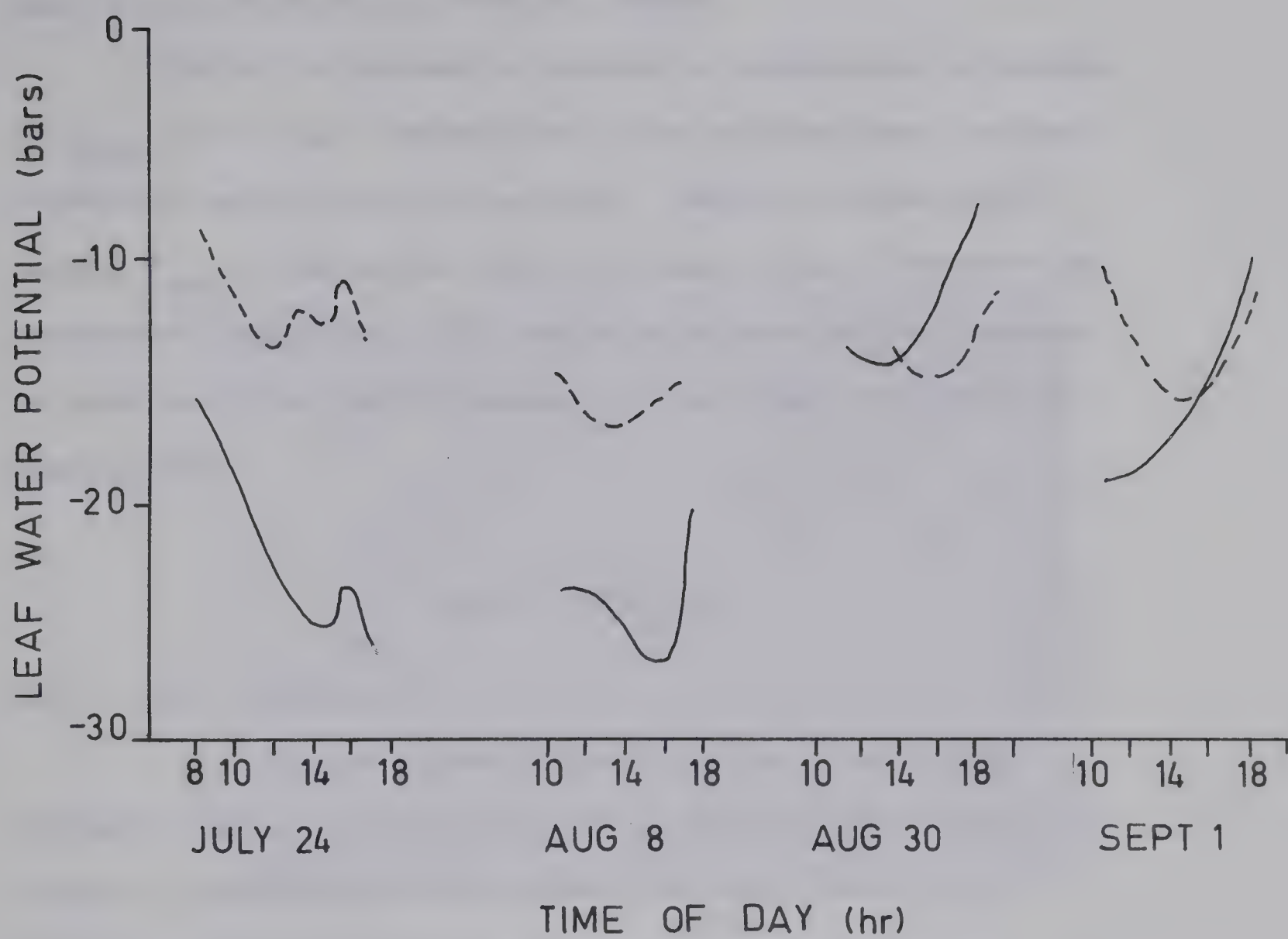


FIGURE 16. Seasonal trend of daily Ψ_{leaf} for *Lupinus* and *Synthyris*.

Lupinus -----

Synthyris —————

bars in a six hour period, than did *Lupinus*.

While Ψ is defined in relation to temperature, no response of Ψ_{leaf} to daily air temperatures, change of cloud cover, or leaf temperature was detected in the field. The data obtained would suggest Ψ_{leaf} is rather the result of longer cycles of moisture and temperature conditions. This conclusion is based on spot readings, although a similar lack of response to temperature is reported by Kramer (1969).

General Morphology

Root to Shoot Comparisons

The two species have different general growth forms. *Synthyris* leaves lay against the ground; *Lupinus* leaves tend to be upright. *Synthyris* roots are somewhat diffuse, arising from a thick rhizome; *Lupinus* roots are derived from a major taproot (Figure 17 shows examples of both root systems; Figures 4 and 5 show above-ground parts.)

Root to shoot ratios, based on oven-dry weight gave values of 1.1:1 for *Lupinus* and 2.7:1 for *Synthyris*. Monk (1965) cites lower values of 0.35:1 and 0.50:1 for perennial herbs in mesic conditions. Volumes of above and below ground parts gave ratios of 1:1 for *Synthyris* and 1:2 for *Lupinus*. A comparison of leaf area to root dry weight gives a 6.8 g root mass for *Lupinus* and 13 g root mass for *Synthyris* per dm^2 leaf area. These measurements indicate *Synthyris* has a potentially greater water absorbing surface per unit leaf area and in general a higher root to shoot ratio. High root to



FIGURE 17: Root system of *Synthyris pinnatifida* (left) and *Lupinus lepidus* (right). Most of the leaves have been removed.

shoot ratios are found in alpine plants (Daubenmire 1941) and in plants growing under dry conditions (Oppenheimer 1960).

Leaves

The leaves of both species are extensively covered with hairs. Hairs on *Lupinus* leaves are quite long and straight; *Synthyris* has shorter and very wooly hairs. Both species have leaves with stomata on both surfaces. The number and size of stomata are affected by environmental factors (Esau 1965, Stalfelt 1959). Because of the difficulty in removing an upper epidermal peel, only one sample was made with *Lupinus* which included both upper and lower stomata counts. This sample of five leaves gave an equal number of stomata, 1 stomata/6.3 epidermal cells or ca. 5300 stomata/cm². *Synthyris* had much smaller epidermal cells than *Lupinus* (78000 cells/cm² for *Synthyris* as compared to 43500 cells/cm² for *Lupinus*) and fewer stomata (1 stomata/22 epidermal cells or 3500 stomata/cm²).

Leaves from plants growing in arid conditions often have a greater number of stomata and a greater number of epidermal cells per unit area than plants growing under more mesic conditions (Stalfelt 1959). That number of stomata per cm² on *Synthyris* and *Lupinus* leaves was much lower (by 1/4 to 1/5) than found on common greenhouse and agricultural plants (from summaries reported in Meyer and Anderson 1952); indicates that neither plant has completely developed the typical morphological adaptations of xerophytic plants. *Lupinus* has a higher number of stomata per surface area, while *Synthyris* has a greater number of cells per leaf area. On this basis it is not possible to rate one more xerophytic than the other. The folded leaflets of *Lupinus* might be considered a xeromorphic trait (Volken, in Oppenheimer, 1961).

DISCUSSION

Alpine Environments

A comparison of alpine environments in the United States, reveals a gradient from summer dry in the West to summer moist in the East. The White Mountains, California are high mountains (3580 m) of the Sierra Nevada. They receive extremely high radiation. Terjung *et al.* (1969) reports, solar radiation reaches 2 ly/min for three to four hours a day on clear July days (which are very common). Net radiation at noon was 1.2 ly/min (approximately equal to solar radiation at noon on Elk Mountain in July); soil heat flux was 0.1 ly/min at the same time. Despite the high radiation, average maximum temperature for July (based on 20 years record) is only 12.5°C. Relative humidity tends to be low, usually less than 50% and winds are light to moderate, 2 to 3 m/sec. Major and Bamberg (1967) report average rainfall to be ca. 4 cm.

Mount Washington in New Hampshire represents the other end of the scale. This area typically has high wind and rainfall, low temperatures and many foggy and cloudy days. Courtin (1968) reports solar radiation from July to average 500 ly/day. Net radiation was 0.54 ly/min and soil heat flux at 0.03 ly/min. on a clear day with intermittent clouds. Average daily temperatures were 9°C; precipitation was 16 cm for the month, based on 29 years' record. Relative humidity is often around 90% and in July 1965, there were 27 days with fog. Winds average 12 m/sec.

Environmental data from Niwot Ridge in the Front Range of the Rocky Mountains (Marr 1965) show this area to be less dry than

the Western mountains. July precipitation averages 7 cm, and cloudy days are frequent. Relative humidity averages 63%. Winds were slightly higher, 4.5 m/sec.

Within this diversity, Elk Mountain is most similar to the White Mountains. Since Elk Mountain is quite a bit lower than the White Mountains (1970 m compared with 3580 m), the solar radiation is lower. Greater cloudiness also reduces the amount of radiation. Winds, temperature, and precipitation are about the same. Net radiation (0.75 ly/min) was intermediate, but soil heat flux (0.26 ly/min) was higher.

Microenvironmental Monitoring

The environmental profiles and the application of the Bowen ratio endeavored to find interspecific differences in response to the environment. This brings up problems of theory and instrumentation.

Slatyer and McIlroy (1961) suggest that the Bowen ratio may be used in an area of vegetation as small as 10 m^2 , provided measurements were made only 50 to 100 cm above the surface (or 10 to 20 cm in cases of severe heating) to avoid problems of advection and eddies. This requirement was met in the profile data in general, but since single plant clumps are as small as 15 cm^2 , with areas of rocky soil surrounding, an insufficient fetch:height ratio could obscure individual plant characteristics. However, differences were detected in the temperature, VPD, and wind profiles for the two species. Nevertheless, no differences were found in the Bowen ratios. This is possibly due to the fact that differences in profiles were concentrated quite near the ground and values for the Bowen ratio calculations were

taken from the upper part of the profile which has become more homogeneous and represents the entire community. The last reason is probably important since the measurements were made with an aspirated sensor which would draw in air from a region greater than the plant.

Despite the objections made by Slatyer and McIlroy (1961), the results of the profiles indicate that differences among various plants can be measured. The use of finer sensors, such as thermocouples, and simultaneous readings closer to the ground would facilitate this.

Water Potentials

Assessments of water deficits can be made by water potential (Ψ) measurements. One such measurement does not reveal much since Ψ is a summation of osmotic and matric potentials and turgor pressure and it also varies greatly among plants (Barrs 1968). However, several measurements can indicate the relative state of water in the plants. Scholander, *et al.* (1965) measured diurnal cycles of 10 to 20 bars and showed a variation in Ψ related to habitat among some forty species in California. Although pattern was monitored only during daylight hours, the two plants showed similar daily range of Ψ_{leaf} . Kuramoto (1968) measured Ψ_{leaf} for several plants in subalpine plants in the Olympics. In general, the subalpine plants had higher Ψ_{leaf} , -9 to -12 bars, compared to -14 for *Lupinus* and -21 bars for *Synthlipsis* in the alpine. Values taken in late August in the subalpine reach ca. -15 bars, much closer to values of the alpine species. There is the suggestion that the subalpine plants are different from those in the alpine in water potentials.

Water potentials are often measured by one or two leaves or

twigs from a plant, but Ψ will vary considerably within a single plant. Water potential for leaves from one *Lupinus* plant showed a range from -19 bars to - 12 bars. The older (three year old) leaves have lower values, -15 bars than did the two year old leaves (-13 bars) or the young leaves (-12 bars). These measurements are based on only ten readings, but show the need for replicate samples. The influence of position could not be determined from the measurements.

Leaf Temperatures

Leaf temperature measurements have been made by many workers as part of energy balance studies. Salisbury and Spomer (1964) recorded leaf temperatures as high as 22°C above ambient under full insolation, and as low as -3.5°C from ambient when in shadow. On Mount Washington, Hadley and Bliss (1964) reported leaf temperatures up to 5°C above ambient. (These values are similar to those reported by Warren Wilson [1957] for arctic plants.) Courtin (1968), also on Mount Washington, measured leaf temperature differences of 16.6°C for a cushion plant on a clear, windless day. On one occasion on Elk Mountain, a departure from ambient of 25°C was recorded. This is higher than previous values mentioned, however, Courtin reported actual leaf temperature at 40°C, whereas the maximum on Elk Mountain was 36°C.

This heating of leaves above ambient temperature can be beneficial to plants in cold regions, such as the alpine or arctic tundra, since metabolic activity depends on temperature. Krog (1955) suggested that hairs on plants, such as the hairs of the willow catkins, prevent the reradiation of heat received by the flowers.

The increased heat available to the flower allows development even when air temperature is below freezing.

Some data were gathered on temperatures of shaved and unshaved leaves of *Agoseris villosa* which has hairy leaf surfaces. Temperatures of leaves which had been shaved were cooler by an average of 2°C than unshaved leaves in 16 to 24 measurements. These data omit one cloudy series where 5 of 6 readings showed the reverse relationship (+20°C). The other measurements were made on generally clear days. The heating of leaves of the two species studied above ambient temperature may be created, in part, by the abundant leaf hairs. This, in addition to evergreen leaves, may play an important role in development early in the growing season.

Plant Adaptation

Since the environment of Elk Mountain ridge is dry from low summer precipitation and loss of snow cover by winds in winter, it is likely water is limiting, at least during portions of the growing season. Results from this short term study would suggest that the two species, *Lupinus lepidus* and *Synthyris pinnatifida*, are adapted to the environment in different ways.

Lupinus appears to be better linked with the microenvironment and available water. The higher values of Ψ_{leaf} imply it can more readily take up water from the soil or it is better able to retain water. The narrower range of ΔT was nearly zero and transpiration high. The wind profiles over *Lupinus*, indicating turbulence over the plant, offer additional dispersal of heat via turbulent transfer. The turbulence is probably the result of roughness created

by the upright leaves (Schmidt, reported in Geiger 1966). Since leaves of *Synthyris* lie close to the ground, turbulence is probably negligible, as indicated by the wind profile. The taproot of *Lupinus* might enable it to get moisture from greater depths, where, at least in spring, there is greater soil moisture. However, it is likely the roots of both species penetrate to bedrock which is often only 50 cm below the surface. Rates of root growth would be useful information for establishing the relative ability of plants to obtain soil moisture. A larger root system or the ability to grow under dry conditions would make more water available (Kramer 1969). The various root:shoot comparisons indicate *Lupinus* is a more mesophytic plant; it has a greater leaf area and leaf mass per mass of roots than *Synthyris*. Generally plants growing under dry conditions have higher root:shoot ratios than plants under moist conditions.

Synthyris appears to be more adapted to dry conditions or more xerophytic; since both live in essentially the same environment, the distinction is largely one of degree. The plant lies low against the ground becoming part of the boundary layer of the ground, minimizing turbulent transfer. The leaves are subject to rather high ΔT 's which suggest transpiration may be limited and not as important in heat exchange as sensible heat must be. The greater proportion of root mass to leaf mass and leaf area is often associated with dry conditions.

The ability of *Synthyris* to withstand high ΔT 's, the larger root mass in comparison of leaf mass or area, and the ability of the plant to maintain low Ψ_{leaf} and grow with low Ψ_{leaf} (both species

produced the new year's leaves in mid-August) might explain why *Synthyris* was able to survive the drought in 1967. Also *Synthyris* flowers in early spring, avoiding more severe drought which increased during July and August, a time when *Lupinus* flowers. The flowers and developing fruits of *Lupinus* could be in competition with the leaves for the limited water (Kramer 1969). Water moves from the soil and plant along Ψ gradients *Synthyris* with lower Ψ_{leaf} might be better able to extract water, when soil moisture became low. Also since *Synthyris* appears to respond to water near the surface, perhaps *Synthyris* might benefit more from a light rain.

There are a number of factors in addition to the differential physiological and morphological adaptations which could also be involved in the death of *Lupinus* and not *Synthyris* in 1967: disease, conditions the previous year when buds are formed, or very likely several of these factors acting together.

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